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THE SEX-LINKED GROUP OF MUTANT CHARACTERS IN DROSOPHILA WILLISTONI

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Introduction

The present work was undertaken for the purpose of comparing the genetical behavior of the fruit-fly *Drosophila willistoni* with that of *Drosophila melanogaster* and other members of the genus. It deals with the 28 sex-linked mutant characters thus far studied. The non-sex-linked characters will be considered in another paper.

Drosophila willistoni Sturtevant (*D. pallida* Williston)[1] is not unlike the well-known *D. melanogaster* in habits and superficial appearance, but a detailed examination reveals numerous features in which it differs from *melanogaster*. Among these are the following: (1) absence of sex combs in the male, (2) six instead of eight rows of acrostichal hairs on the thorax, (3) smaller size and more slender form, (4) vermilion instead of red eye color, and (5) narrow instead of broad bands on the abdomen.

This species has been chosen for the present study because it is one of the species having the same general type of chromosome group as *D. melanogaster*. It will be recalled that within the genus Drosophila at least eleven different types of chromosome groups are represented (Metz, 1916). The most common type is that called type A (Fig. *A*, present paper), which is found in 13 of the 29 species studied. In these 13 species (which include *melanogaster* and *willistoni*), the chromosome groups are so much alike as to suggest that similar chromosomes are homologous and carry homologous groups of genes throughout. On the other hand, the species themselves do not form a restricted taxonomic group, but seem to be scattered more or less at random through the genus—which does not conform to such a view unless this type of chromosome group be considered primitive and the forerunner of several other types.

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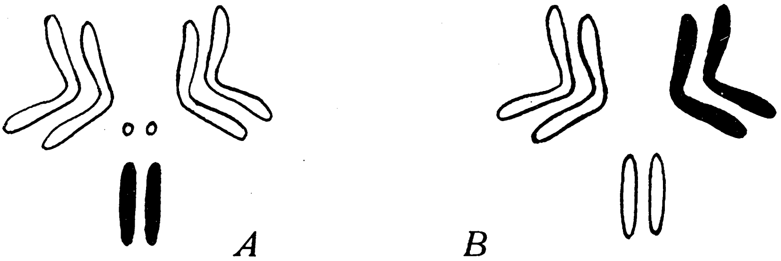
[1] See Sturtevant, 1921*b*, for description, etc.

These considerations indicated the need of a comparative study of different species possessing this type of chromosome group, in addition to the studies already being made on species having different types of groups. Since the species can not be hybridized (or have thus far refused to hybridize—with one exception considered below), it is necessary to make cytological and genetical studies of them individually. This of course limits the comparison to a very few species.

The present paper supplements our previous one (Lancefield and Metz, 1921) on the sex chromosome relationships of *willistoni* and *melanogaster,* in which it was shown by means of non-disjunctional flies that the sex chromosomes are not strictly homologous in the two species. In *melanogaster* the short, rod-like pair is the sex chromosome pair (Bridges, 1916), whereas in *willistoni* we find that the rod-like pair is an autosome pair, and that one of the large V-shaped pairs is the sex chromosome pair. This relationship is shown in Figs. *A* and *B*.



FIGS. *A* and *B*. Diagrams of female chromosome groups of *Drosophila melanogaster* and *Drosophila willistoni* respectively. The X-chromosomes are represented in solid black, the autosomes in outline. In *D. willistoni* the small, dot-like pair may be absent.

The genetical study considered here is for the purpose of comparing the constitution of the sex chromosomes by means of the sex-linked characters and their linkage relations.

The stock of *D. willistoni* which we have used was brought from Cuba in 1915, and was kept in the laboratory without being studied until 1919 when the present work began.

In making the tests for linkage and in calculating crossover values, the usual procedure has been followed.[2] We have been concerned particularly with determining the relative order of the genes and the approximate amount of crossing over between them, but not with obtaining exact crossover values. In consequence, the " chromosome map " given here is to be considered as indicating only the approximate location of the respective genes.

In presenting the data, the mutant types are described, not in chronological order, but in such a way as to follow the serial order of the genes on the chromosome map. All of the sex-linked characters are recessive. The data on the origin of mutants are necessarily imperfect, and in some cases are very meager, owing to the fact that many of the mutants appeared in stock cultures, mass cultures, etc., for which no complete records were taken. In such cases the available data are given briefly under the appropriate headings.

We are indebted to Mr. D. E. Lancefield for carrying out some of the early experiments, and for finding the mutants "rimmed" and "nicked." Similarly, we are indebted to Miss Ruth Ferry for the mutant " yellow " and for carrying out the experiments involving " yellow." To Dr. A. H. Sturtevant we owe many valuable suggestions regarding the comparison of mutant characters in *D. willistoni* with those in *D. melanogaster* and *D. simulans*. We are also indebted to the following persons for making the accompanying drawings: Miss Ruth Lincks — Figs. 1, 3, 7, 8; Mrs. D. B. Young — Figs. 2, 4, 5, 6, 17; Miss E. M. Wallace — Fig. 9, and Miss E. D. Mason — Figs. 10 - 16.

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[2] This has been described in earlier papers by Morgan and others, and is to be found in current books on genetics.

DESCRIPTION AND ORIGIN[3] OF MUTANT CHARACTERS

Stubby (*sy*)

Description.—Stubby is a bristle character, manifested by all of the thoracic and head bristles (Fig. 2). These are usually shortened, thickened, and somewhat curled, and often are split or forked at the tip. The two posterior scutellar bristles are frequently tightly twisted together and point anteriorly. The short, thick appearance of the bristles is never apparent in combination with small-bristle, but the character can always be distinguished by the forking of the sternopleural bristles. Both sexes are fertile. Stubby looks very much like forked in *melanogaster*.

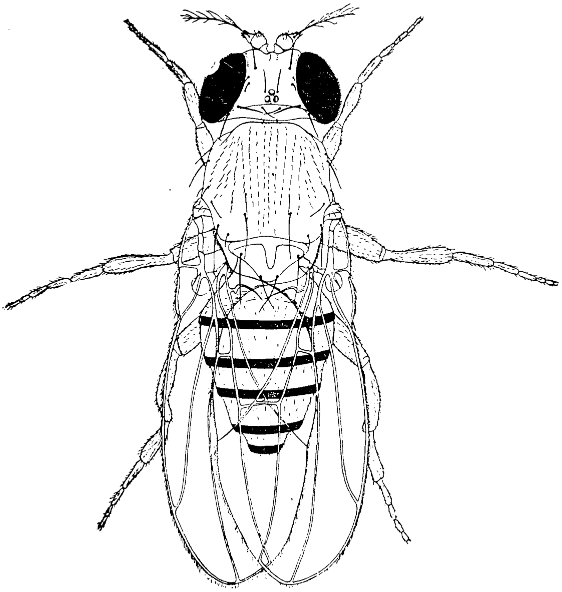

FIG. 1. *Drosophila willistoni*, "normal."

Origin.—One stubby male was obtained from a pair mating. No complete record of this culture was kept, however, and it is not known whether others appeared previously or not.

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[3] See Table I.

Orange (*o*)

Description.—The eyes are orange colored. In newly hatched flies, the color is a pale lemon, which deepens into orange as the fly matures and may become very dark in old age. The color resembles garnet or coral of *D. melanogaster.*

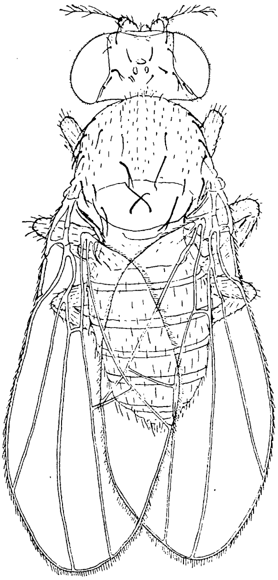

FIG. 2. Stubby, bristles.

Origin.—One male appeared among the offspring of a mating of three normal females by an unrelated male. The other offspring were all normal, but their number was not recorded. Presumably, the mutation occurred in one of the P_1 females and affected only one or a few germ cells, although it is possible that this female was heterozygous and produced a very small number of the flies in the culture.

Small-bristle (*sb*)

Description.—All the bristles are more slender and somewhat shorter than in normal flies. The character is extreme when orange eye color is also present.

Origin.—One small-bristle, forked male was obtained from a mass culture carrying rough and forked.

More than a year later, a second mutation to small-bristle occurred in an entirely unrelated stock. In this case the single small-bristle male found among the offspring of one pair was crossed to a female from a homozygous orange small-bristle stock and produced only small-bristle flies.

Bent (*bn*)

Description.—The wings of bent flies are slightly spread out, and are bent at the base so that they slope down toward the body (Fig. 3). They are often slightly crumpled. The flies hatch as well as their normal sibs but do not breed as readily.

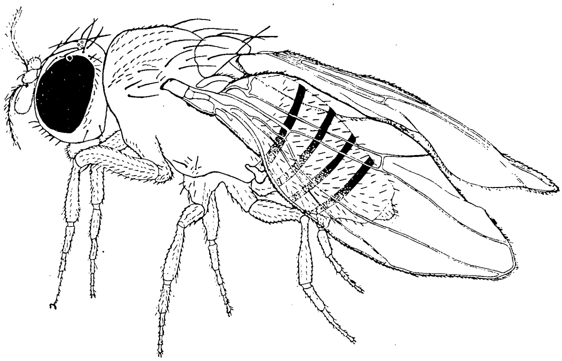

FIG. 3. Bent, wings.

Origin.—Many bent males were found in a culture of five orange females from stock mated to a single male of different parentage. At least one of the females carried bent, but the exact origin is uncertain. No bent flies were ever observed in orange stock.

Forked (*f*)

Description.—In forked flies, all the bristles are wavy with the ends sometimes forked. The females are sterile. This character is similar to, but less extreme than, stubby. It recalls singed$_2$ of *melanogaster* although singed$_2$ is slightly more extreme.

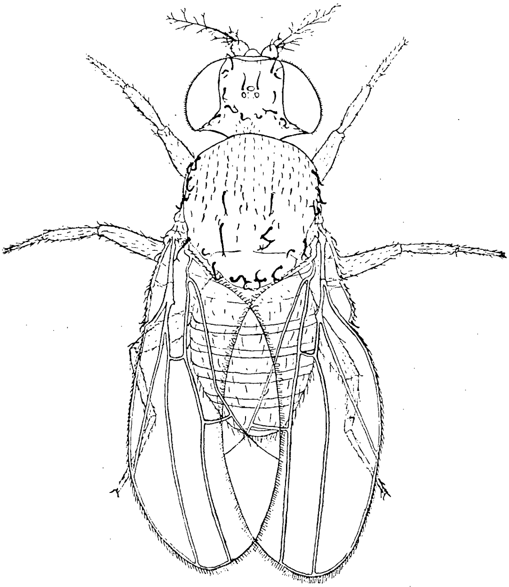

FIG. 4. Forked-2, bristles.

Origin.—Seven males were found in a stock bottle. Since no forked females were obtained, it is possible that this was the original appearance of the mutant and that all of the forked flies were from one mother, heterozygous for forked.

Forked-2 (f_2)

Description.—This character is much more extreme than its allelomorph, forked, or the similar mutant, stubby. The bristles are twisted and thickened with their ends often split (Fig. 4). The twisting also affects practically all the hairs on the fly, including those on the inner margin of the wing. The hairs on the antennæ are forked. Forked-2 resembles the *melanogaster* singed. The females are sterile.

Origin.—Several forked-2 males and one female appeared in a stock bottle of small-bristle flies.

Tiny (*t*)

Description.—Tiny-bristle flies usually have small anterior dorso-central bristles. Sometimes the two anterior scutellar bristles are also small. Occasionally all the bristles may be small, so that the individual may be indistinguishable from a true "small-bristle" fly. The character is rather variable and, in many cases, is very hard to separate from normal. This difficulty was so great that the stock was finally discarded.

Origin.—A single male was found on the last count of the offspring from a pair mating. It is possible that other tiny males were present among the previous offspring and escaped observation since the character is very inconspicuous.

Square (*sq*)

Description.—The wings are about two thirds the normal length with the ends almost square instead of pointed (Fig. 11). A characteristic slight wave extends throughout the length of the wing. The females are sterile and the viability of the males is rather poor.

The description of square suggests that of rudimentary *melanogaster* but square is much less extreme than rudimentary; the wing is not shortened so much and is not cut off so squarely.

Origin.—Among the offspring from a pair mating (rough female by orange rough stump male) several square males were found, indicating that the mother was probably heterozygous for square.

Reduced (*re*)

Description.—Reduced flies regularly lack the two anterior dorso-central bristles; occasionally, they also lack one of the posterior dorso-centrals; and less frequently, all four are absent. In combination with scute-2, however, the more extreme condition of reduced is frequently found (Fig. 7). The reduced gene also affects the shape of the abdomen, which is blunted, or apparently compressed along the anterior-posterior axis. The abdominal bands are slightly irregular.

Reduced flies, especially females, are hard to breed in pairs, although those which do produce offspring seem normally fertile.

Origin.—Many males were found among the offspring from a pair mating from orange stock. The mother of the culture was apparently heterozygous for the gene.

THE SCUTE ALLELOMORPHIC SERIES

1. *Scute* (*sc*)

Description.—The two anterior scutellar bristles are usually lacking, although occasionally only one may be gone. Rarely the combination of one anterior scutellar bristle and one posterior one may be found. The remaining bristles are normal in size. The character almost always manifests itself in homozygous flies. Only one exception to this has been detected up to the present time.

Origin.—Fifteen scute males and eleven normal males were obtained from a normal pair. The female offspring were all normal (number not recorded). It is almost certain that the mother was heterozygous in this case, and that the mutation occurred in a previous generation or else very early in her own ontogeny.

2. *Scute-2* (sc_2)

Description.—Scute-2, an allelomorph of scute and scute-3, involves the same scutellar bristles as scute, but varies toward a more extreme condition than this allelomorph. The two anterior scutellar bristles are always missing, frequently one of the posterior scutellars is gone, and occasionally all four are lacking. The bristles on the scutellum are fine and small. In a stock homozygous for reduced and scute-2, both characters are more extreme than either is alone (Fig. 7). Such flies often entirely lack dorso-central and scutellar bristles, and lack one or more orbital bristles.

The compound scute scute-2 females are either somewhat intermediate between the two, or they may look entirely like one or the other component. On the whole, they are more apt to resemble scute-2 than scute.

Origin.—From a normal female mated to a scute male, the following types of offspring were obtained: males — one half normal, one half scute-2; females — one half normal, one half somewhat intermediate between scute and scute-2. From this it was concluded that the parent female was heterozygous for the new character and that this character was allelomorphic to scute, a conclusion subsequently verified by direct tests. Six sisters of this female were also tested and none gave scute-2.

3. *Scute-3* (sc_3)

Description.—Scute-3 is an allelomorph of scute and scute-2. All four scutellar bristles, the two sterno-pleural bristles, and a varying number of head bristles are absent. On the head, all three pairs of orbitals are usually missing, and occasionally some of the others are gone.

The compound females involving scute-3 and scute-2 are more apt to be like scute-3 than like scute-2, although in general they are intermediate. Such females could be distinguished from the homozygous scute-2 females in all the cases observed by the absence of at least one sterno-pleural bristle and generally by the absence of all scutellar bristles. Scute-3 males are sterile.

Scute-3 strongly resembles the scute of *melanogaster*. In both cases scutellar and head bristles are affected. Two stocks of *melanogaster* scute kindly examined by Dr. Sturtevant agree with scute-3 in lacking scutellar bristles and orbitals, and in having small ocellar bristles. They both possess post-orbitals, however, and one stock occasionally shows the middle orbital present. The other usually lacks the postverticals.

Origin.—Scute-3 was first observed in the offspring of an F_2 female from a cross of a scute female from stock by two rough rimmed stump males. This female seemed to be heterozygous for the new factor, and it was found that the character was also present in males in sister cultures which had been used for stocks.

Yellow (*y*)

Description.—In "yellow" flies the body, wings and legs are deep yellow. The bristles and hairs are all yellowish or bronze instead of black. In the latter respect yellow differs from the yellow in *Drosophila virilis* which has black or dark brown bristles and hairs.

Origin.—A single yellow male appeared in a bottle of scute rough stump stock.

Yellow was found after the main part of this paper was prepared for publication, and since the experiments involving it have not added materially to the data given in the tables they are omitted from the latter and are given briefly here.

The original yellow scute rough stump male was mated to normal females giving a normal F_1. The latter, inbred in pairs, gave 1354 normal daughters and the following classes of sons: normal 488; yellow scute rough stump 466 (non-crossovers 954); yellow scute 25, rough stump 23 (single crossovers in region two 48); yellow scute rough 49, stump 46 (single crossovers in region three 95); yellow scute stump 3, rough 2 (double crossovers involving regions two and three, 5). In addition, two yellow rough stump males and one yellow stump male were obtained. Of the former, one proved to be genetically scute when tested and hence should be in the non-crossover class. The other gave no progeny, but presumably was also a non-crossover. The third fly likewise failed to breed, but since it lacked rough as well as scute it presumably represents a double crossover in regions one and three. It is this fact which leads to the tentative location of yellow above rather than below scute on the map.[4]

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[4] This is supported by subsequent data.

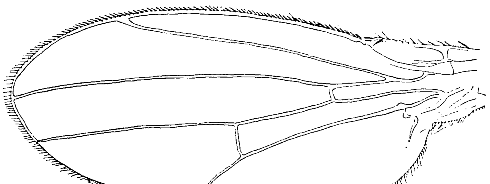
Peach (*p*)

Description.—Peach eye color is practically indistinguishable from orange eye color, although, as a rule, it is a trifle darker than orange and does not have the range of shades due to age which are observed in orange. In the same culture, it is impossible to distinguish the two with certainty. The double recessive of peach and orange is probably indistinguishable from either eye color alone. Homozygous peach rough flies have darker eye color than orange rough flies, and are hard to separate from rough alone. Peach eye color is similar to ruby and garnet of *melanogaster* and to rubyoid and carmine of *simulans*.

Origin.—A single male with peach eye color was found in a double recessive forked stump stock.

Beaded (*be*)

Description.—Beaded refers to the condition of the wings, which have the marginal hairs clumped in irregular patches, especially on the posterior half of the outer margin. The wings are pointed at the ends due to a long notch, extending from the tip of the third vein to about



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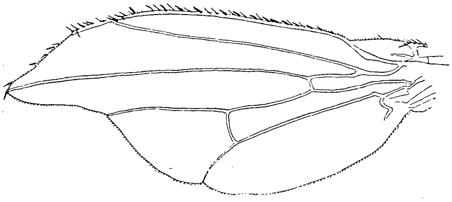

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FIG. 5. Normal, wing.
FIG. 6. Beaded, wing.

the region of the posterior cross-vein, and to the loss of a section from the outside of the wing between the distal ends of the second and third veins (compare Figs. 5 and 6). Beaded flies have poor viability, and the females are sterile. Beaded is similar in appearance to the *melanogaster* cut$_6$ although the latter is slightly more extreme than beaded. While cut$_6$ flies are vigorous and fertile, some of the cut allelomorphs are not completely fertile and have poor viability.[5]

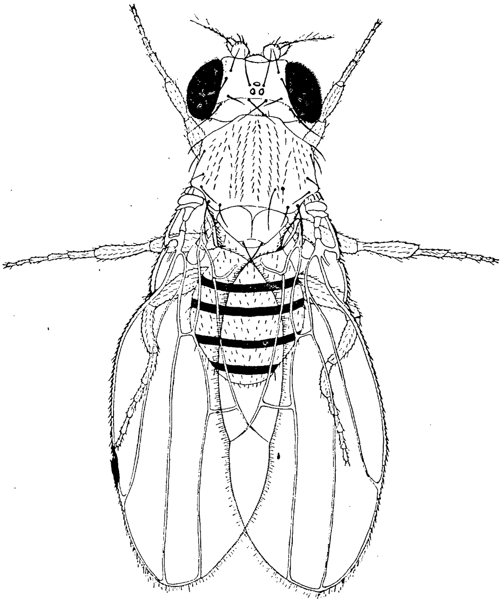


FIG. 7. Reduced scute-2 compound.

Origin.—An out-crossed female, known to carry small-bristle rough on one X-chromosome, and small-bristle orange short-3 on the other, produced offspring in which the small-bristle rough males were also beaded. This female was almost certainly heterozygous for the new gene. Nine sisters were bred separately but no beaded flies appeared in their offspring.

[5] Unpublished data for which we wish to thank Drs. Mohr and Bridges.

Rough (*r*)

Description.—Rough eye affects mainly the surface of the eye (Fig. 8). When the outer portion of the eye is mounted and examined under the high-power microscope it is seen that the ommatidia are irregular in shape and size with uneven surfaces which are more convex than the normal. The normal eye has regular hexagonal facets with a bristle at every alternate intersection of the sides (See Carnegie Publ. 278, Plate 10, Fig. 3*c* for the normal eye of *D. melanogaster* which has the same arrangement). The bristles of rough eye are irregularly distributed with groups collected in one place and no bristles at all in another. These bristles are about one and a half times the length of the normal ones.

The roughened condition is similar to that found in star eye of *melanogaster* (Carnegie Publ. 278, Text-figure 83). The eyes of *willistoni* rough are also somewhat glossy in texture, and the wing veins are slightly heavier than in the normal flies.

Origin.—Several rough males and females were found in one of the bottles of a stock that had been kept in the laboratory for approximately four years. It is probable that the mutant gene had been present in the stock for some time.

Triple (*tr*)

Description.—Triple causes four variable wing changes, one or all of which may be present in either or both wings (Fig. 10). (1) The second and third veins may be fused for a short distance at their origin. (2) The wings, slightly tilted up at the ends, are held away from the body at an angle which varies up to about 90°. (3) The third veins fail to reach the distal margin of the wings by amounts which vary from almost nothing to one third the length of the vein. This is particularly evident in the females, where a large section may be missing from the central part of the third vein. (4) An extra cross-vein is present between the second and third veins at a level about half way between the anterior and posterior cross-veins. This vein, when not wholly formed as a cross-vein, is often indicated by short pieces of disconnected vein.

The fusion of the second and third veins and the extension of at least one wing are constant characters as far as observed. The latter forms the easiest basis of distinguishing this mutant. The females are more extreme than the males in all four of the changes involved. Triple suggests the *melanogaster* mutant, bifid, by its extended wings, fusion of the veins at the base of the wing, and the shortening of one of the veins, although the short vein is the fourth in bifid and the third in triple and the third vein of bifid is thickened at the distal extremity.

Origin.—Triple was first noticed in the offspring of a female out-crossed from wild stock. Half the males were triple. On investigation it was found that several bottles of wild stock contained similar males.

Triple males were found six months later in stump stock. Crossed to the original triple stock, these males produced triple female offspring in the F_1 generation. The possibility of contamination of the stump stock can be eliminated since the triple males found in the stock were also stump, and there were no cultures containing triple stump flies in the laboratory.

THE DEFORMED ALLELOMORPHIC SERIES

1. *Deformed* (*d*)

Description.—Deformed, which involves many parts of the body (Fig. 9), shows sexual dimorphism. In the male the eye is about two thirds the normal size and very rough; in the female the eye is normal in size and only slightly roughened. In both sexes the bristles are abnormally long and irregularly bent. The thoracic hairs are badly disarranged in both sexes, but the effect is very much more exaggerated in the female than in the male. In the former, the hairs are often clumped in a compact mass on the anterior half of the thorax; while in the male, the hairs are irregularly scattered over the whole area. The scutellum in the male (sometimes in the female also) is blunt instead of pointed, posteriorly, and the under portions of the thorax are consequently visible. The wings are extended at an angle of about 45° to 90° in both sexes, and the veins are often faint, short, and irregular, especially in the male.

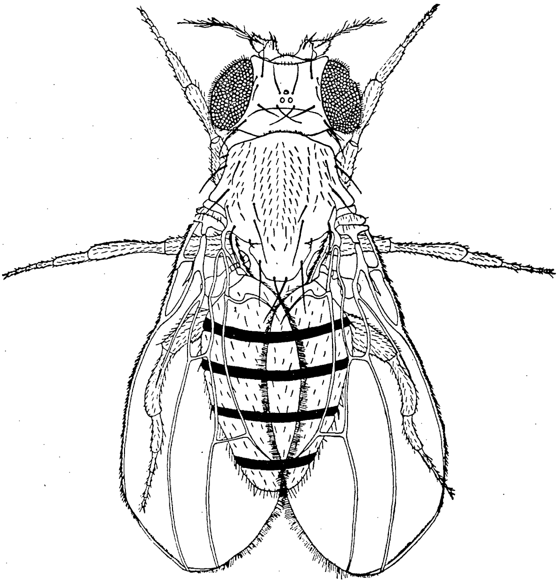


Fig. 8. Rough (eye), rimmed (wing margin), stump (second wing vein) compound.

These flies are rather feeble and breed poorly except in mass culture, probably on account of the many physical defects present.

Origin.—Many males and females were found in a stock culture of orange forked rough. Sister bottles made up at the same time did not produce any deformed flies.

2. *Serrate* (*st*)

Description.—Serrate is an allelomorph of deformed, but involves only a part of the characters modified by deformed. The changes in the eyes of the two sexes are exactly the same as those caused by deformed. On the other hand, the bristles and the shape of the scutellum are almost normal and the thoracic hairs are only slightly disarranged. The wings may occasionally be held at an angle with the body, but the venation is practically normal. The only strikingly noticeable effect of serrate is the change in the eyes.

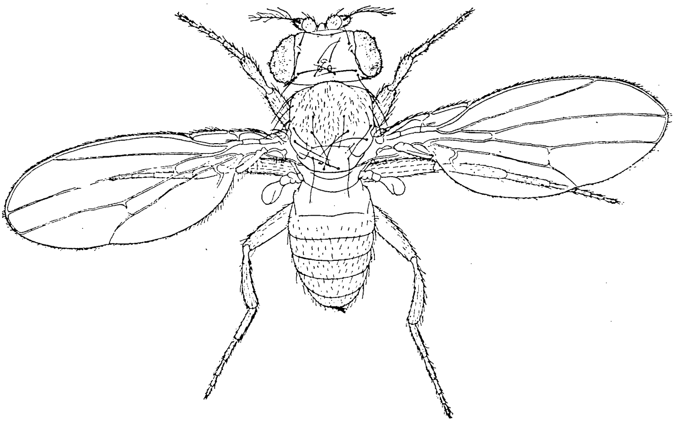


FIG. 9. Deformed ♂.

The compound deformed-serrate females are intermediate between the two allelomorphs but tend to resemble serrate more closely than deformed. Serrate flies are more viable than deformed and breed more readily.

Origin.—A single male was found in an F_2 mass culture from a mating of two females by one male from scute stock. No other serrate flies appeared in this culture or in a sister culture.

Rimmed (*ri*)

Description.—In rimmed flies, a heavy rim of marginal hairs surrounds each wing and the wings curve down over the abdomen as if the margins were constricted (Fig. 8). The depression between the scutellum and thorax of normal flies is eradicated, leaving a smooth surface at the junction. The thick marginal rim of hairs is the most constant of the effects of rimmed, but the other changes are usually apparent.

Origin.—Several males were found in wild type stock.

Pale (*pa*)

Description.—The post-vertical and all the thoracic bristles are pale yellow. Occasionally, a few other head bristles are also yellow. The bristles are thin, and the entire fly is weak and small with the wings often not unfolded. None of the original pale flies could be induced to breed. The heterozygous females produced a few pale offspring, but the stock was soon lost.

Origin.—The mother of the culture in which pale appeared was heterozygous for scute rimmed on one X-chromosome and for pale morula on the other. Five sisters of this female were bred, but no pale offspring were obtained from any of them. It is impossible to tell whether the mutation to pale occurred in the mother of the culture in which pale was found or whether it took place in her mother.

Stump (*s*)

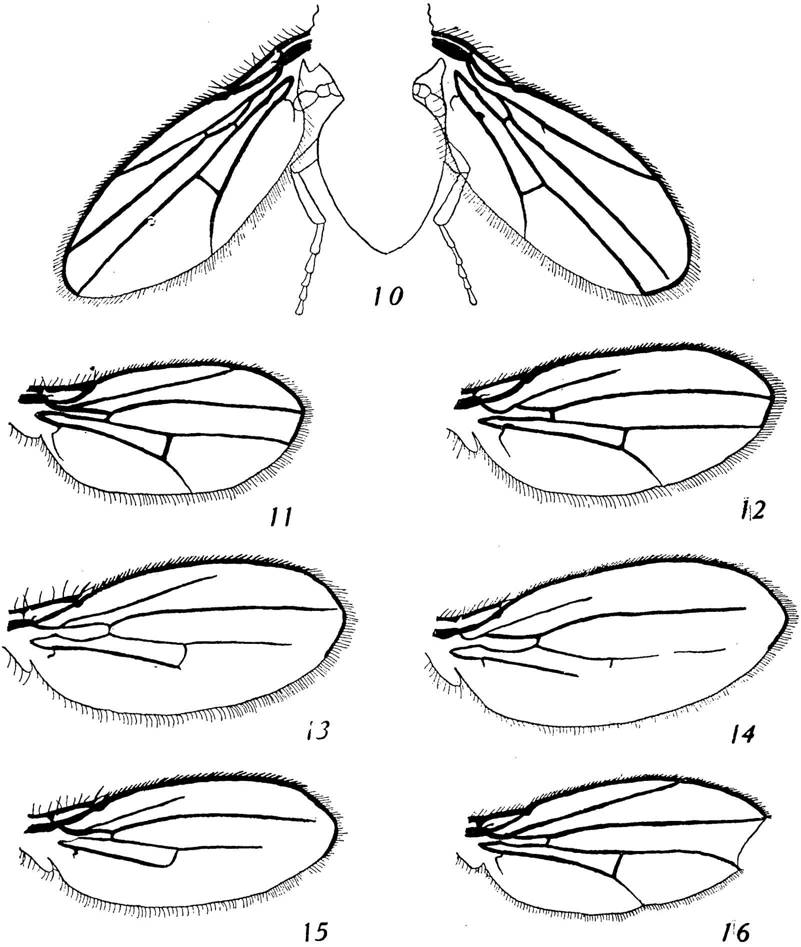
Description.—The distal portion of the second vein is lacking, leaving only a stump at the base of the wing (Fig. 12). This stump varies in length from one quarter to two thirds that of the normal vein.

Origin.—Six stump males were obtained from a mass culture in which the mothers were heterozygous for forked and the fathers were normal. Four of the stump males were also forked, the others were not.

THE SHORT ALLELOMORPHIC SERIES

1. *Short* (*sh*)

Description.—Typically, all the veins of the wing fail to reach the margin in short flies, although sometimes the third vein is entire (Fig. 13). The second vein is shorter than any of the others. Ordinarily, the distance between the ends of the veins and the margin is not great. The posterior cross-vein is broken occasionally.



FIGS. 10–16: Fig. 10, triple. Fig. 11, square. Fig. 12, stump. Fig. 13, short ♂. Fig. 14, short-2 ♂. Fig. 15, short-3 ♂. Fig. 16, nicked.

Origin.—Short was first observed in half the sons of a single female indicating that the mother was heterozygous for the short gene. This female carried orange rough on one X-chromosome and stump on the other. The mutation to short evidently affected a locus of the orange rough chromosome not far from the stump locus. Several sister cultures were examined, but no short flies were found.

2. *Short-2* (sh_2)

Description.—Short-2 is the most extreme of the series. In the females the second, fourth, and fifth veins are very short, the fourth and fifth often not reaching as far as the posterior cross-vein. In cases in which they extend beyond the cross-vein, this vein is broken. In the males the fourth and fifth veins are about three quarters the normal length, and the posterior cross-vein is broken (Fig. 14). The males are indistinguishable from those of short-3.

Origin.—A single male was found in small-bristle rough stock.

3. *Short-3* (sh_3)

Description.—Short-3 is about the same in both sexes (Fig. 15). The second vein is very short, and all the others are about three quarters the normal length. The posterior cross-vein is usually broken.

Females containing any two of these three allelomorphs are intermediate between the two used, with perhaps a closer resemblance to the more extreme member of the pair.

Origin.—Several males were found in scute stock.

Morula (m)

Description.—Morula involves a partial roughening of the eyes which is due to a consolidation of a group of facets, especially in the central area of the eye, suggesting the lozenge of *melanogaster*. The viability of this stock is very poor, and the double recessives of morula and any other mutant character rarely survive.

Origin.—At least five males were obtained from a mass culture of three pairs which carried rough. The classification of rough and morula was not accurate at its first appearance.

Nicked (*nk*)

Description.—Nicked is characterized by irregular notches in one or both wings (Fig. 16). The indentations vary in size and location, but tend to show on the posterior and inner portions of the wing. In certain lines, the character shows regularly, while in certain other lines it overlaps normal a great deal. Flies in which nicked is combined with other mutant characters have rather poor viability.

Origin.—Several individuals of both sexes were found in a mass culture.

Rosette (*ro*)

Description.—In this mutant race, a large number of characters are affected (Fig. 17). The eyes are slightly roughened due to disarrangement of the facets; the thoracic hairs are disarranged, looking as if they had been brushed in the wrong direction; the bristles may be bent; the distal tarsi of the legs may be twisted; and the wings are generally held at an angle with the body, and one or both may be small and circular. The rough eyes and disarranged hairs are constant characters. Rosette flies have very low viability and are hard to breed, especially when other mutant characters are present also.

Origin.—Four rosette rough males were obtained among a large number of offspring from one morula male by three rough females.

CONSTRUCTION OF THE X-CHROMOSOME "MAP"

With one or two exceptions the usual procedure[2] has been followed in constructing the chromosome "map." The order of the genes was determined by means of crosses involving three or more loci (Tables III–VI), and that order adopted which, in the consideration of any three points, made the double crossover class the smallest. In most cases the decision was confirmed by several subsequent experiments made for other purposes. Tiny and square have not been definitely located with reference to forked since they proved unsuitable characters for use in linkage experiments. Similarly, the loci of triple and deformed are known to be between rough and rimmed, but the relative positions of the two could not be determined on account of the impossibility of using the two characters together. Pale, morula, and rosette are also only tentatively placed.

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[2] See footnote, p. 213.

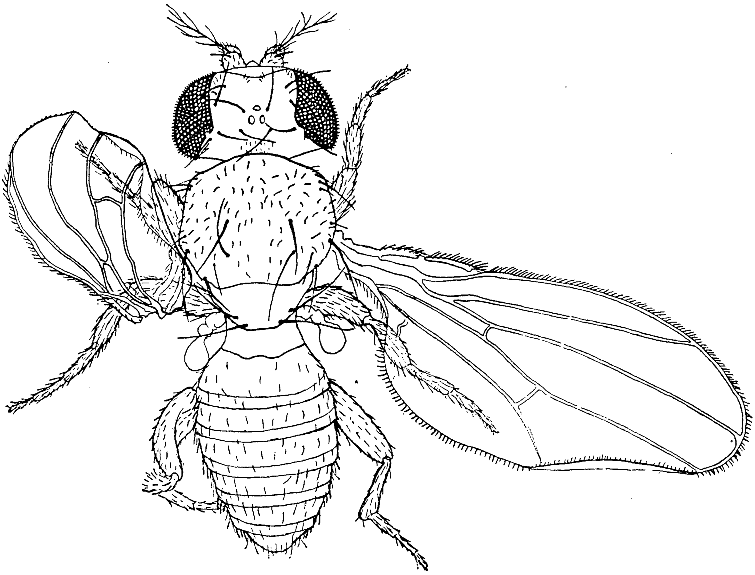

FIG. 17. Rosette.

With the order of the genes established, the "distances," or crossover values, between them were obtained by combining the data from all the experiments given in Tables II–VI. Table VII gives the summary of all data between any two loci in the "map" from those experiments in which no intermediate genes were concerned. This differs from the usual method of summarizing the data in that it includes only experiments in which no intermediate point was used.

As far as possible the positions of the genes on the "map" have been determined by summation of the "distances" between neighboring loci taken in pairs, using stubby arbitrarily as the zero point. In several cases, however, the locus of a gene has been assigned by reference to some main well-established point; notably, orange, forked, scute, rough, or stump. In Table VII, the starred data are those on which the "map" is based. No correction for data involving non-adjacent loci has been made, since the degree of numerical accuracy does not warrant such a computation in this case. No correction has been made for double crossing over in long regions in which no mutant loci are known.

Owing to the possible parallelism between the yellow and scute in *willistoni* and the yellow and scute in *melanogaster* a second set of readings has been given on the "map" using the position of yellow as the zero point and plotting the others in opposite (+ and —) directions from this. Comparison with the X-chromosome map of *melanogaster* is thus facilitated.

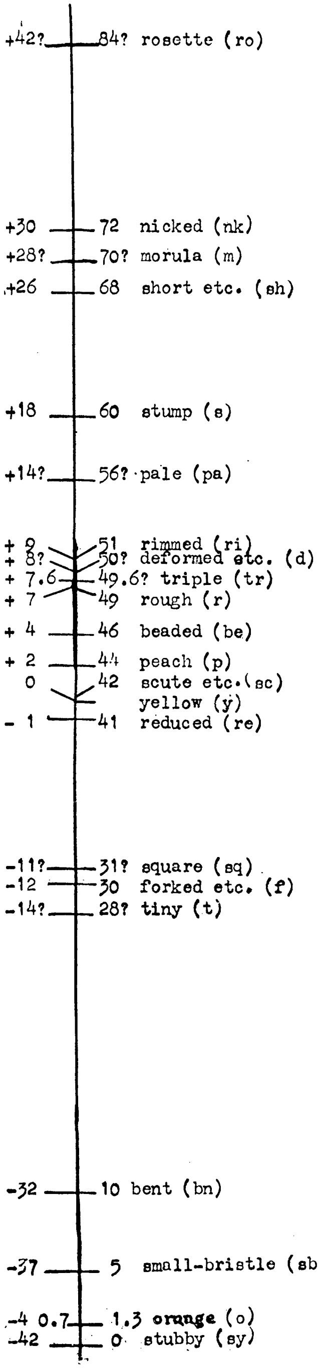

FIG. 18. Map showing linkage relations of sex-linked genes in *Drosophila willistoni*.

DISCUSSION

The previous work on the comparative genetical study of different species of Drosophila has been concerned largely with species having different types of chromosome groups. It has involved mainly the species *melanogaster, virilis, funebris, simulans* and *obscura*. Of these, only *melanogaster* and *simulans* have the type of chromosome group with which we are concerned here. The published data on the first four of these species have recently been summarized by Sturtevant (1920) and may be passed over briefly. The data on *obscura* are in press and our references to them are made with the kind permission of Mr. D. E. Lancefield.

In *melanogaster, virilis, funebris* and *obscura*, the evidence suggests a tendency on the part of each species to give mutants paralleling those in the others, although the extent of this tendency can not be ascertained accurately because of the impossibility of proving the homology of similar characters. In the case of *melanogaster* and *simulans* the parallelism extends to nearly all of the known *simulans* characters and certain homologies are established by means of hybridization (Sturtevant, '20, '21*a*, 21*b*). To be sure, the two latter species are almost identical and would be expected to give similar genetical results; but it is of interest to note that there is a close resemblance between the proven cases of parallel characters in these, and the apparent cases of parallel characters in the other species. This tends to increase the probability of actual parallelism in the latter where a series of linked characters is involved.

Upon comparing the mutant characters of *willistoni* with those of the others it is evident that only a few striking cases of resemblance are found. Of these the most significant involve the characters yellow and scute. Their morphological resemblances to the yellow and scute in *melanogaster* have already been noted in the descriptive section. But the evidence for their being parallels is made particularly strong by the fact that their genes are completely or almost completely linked in both species. In *melanogaster* yellow and scute are located at the extreme end (zero point) of the chromosome map, while in *willistoni* they are approximately in the middle.

A situation similar to this has already been found in *D. obscura* (according to unpublished data of D. E. Lancefield). Here the characters yellow and scute also bear a close resemblance to those in *melanogaster* and are very closely linked. As in *willistoni,* the factors for yellow and scute are near the middle of the chromosome map. It will be recalled that *obscura,* like *willistoni,* has a large V-shaped X-chromosome—although the other chromosomes are different (Metz, 1916). In the two species having V-shaped X-chromosomes, then, yellow and scute are "located" near the middle of the chromosome map, while in *melanogaster* with its short, rod-like X-chromosome, yellow and scute are at one end. As Lancefield has pointed out in his discussion of *obscura,* this suggests that one end of the rod-like X in the one case corresponds to the middle of the V-shaped X in the other. And this suggests that the rod-like chromosome itself may correspond to one arm of the V.

The only evidence in *willistoni* on the latter hypothesis is that furnished by the characters forked and stubby. These are possible parallels of the singed and forked in *melanogaster.* They are similar in a general way in the two species (see description above), and the serial order of the genes is the same (Fig. 18), although the linkage relations do not agree exactly.

In this connection it may be recalled that "yellow," "singed" and "forked" have also been found in *Drosophila virilis* (Metz, 1918, and unpublished data), and may, likewise, be considered as possible parallels to those in *melanogaster.* *Virilis* has a rod-like X-chromosome resembling that of *melanogaster,* and the relative positions of the three genes on the chromosome map resemble those in *melanogaster*. Yellow is about three units from the end instead of at the end; singed is at about 35 instead of 21 and forked is at about 58 instead of 56.5.

The evidence is not sufficient to warrant the conclusion that these are actually homologous series, but the fact that such series exist suggests that by the present means it may eventually be possible to obtain reliable data for a comparison of the chromosomal make-up of the different species.

Among the other characters in *willistoni* which show some resemblance to characters in *melanogaster* or *simulans* the following may be noted as a matter of record, although there is little indication of their being actual parallels: orange and peach (which look alike) resemble coral or ruby; beaded is similar to the cut allelomorphs both morphologically and in respect to its sterile females and poorly viable males; triple suggests bifid, and morula looks like lozenge. The small bristle of *willistoni* may be comparable to the tiny bristle-2 of *simulans*.

The fact that the X-chromosomes in *willistoni* are morphologically like the large autosomes and not like the X-chromosomes of *melanogaster* suggests that we ought to compare, not only the sex-linked groups of the two species, but also the sex-linked group of *willistoni* with the non-sex-linked groups of *melanogaster*. This has been done, but without revealing any significant indication of parallelism.

In conclusion it may be noted that although the evidence is not yet clear on the genetic relationship of the sex chromosomes in *melanogaster* and *willistoni*, yet if the above suggestion is correct, that the X-chromosome of *melanogaster* corresponds to part of the X-chromosome in *willistoni*, then the resemblance between the chromosome groups of the two species is only superficial. It may also be noted that the genetic ''map'' of the X-chromosome of *willistoni* at present is only slightly longer than the map of the *melanogaster* X-chromosome (84 as contrasted with 70 units), whereas the *willistoni* X-chromosome itself appears to be about twice the length of that of *melanogaster*. This suggests that crossing over is less frequent in *willistoni* than in *melanogaster*.

SUMMARY

1. Twenty-eight recessive sex-linked mutant characters in *Drosophila willistoni* are described and their linkage relations considered.
2. In general, the genetic behavior of *willistoni* (as regards crossing over, etc.) is similar to that of *D. melanogaster* and the other species of Drosophila whose genetic behavior is known.
3. There is a strong indication of parallelism between the mutants yellow and scute in *willistoni* and yellow and scute in *melanogaster*.
4. In both species these characters are completely or very closely linked.
5. There is some indication of parallelism between the characters forked and stubby in *willistoni* and singed and forked in *melanogaster*.
6. In *melanogaster* the genes for yellow and scute are "located" at one end of the chromosome map, and singed and forked are 21 units and 56.5 units respectively from this end. In *willistoni* yellow and scute are near the middle of the map, and forked and stubby are on one side at 12 units and 42 units respectively.
7. Since the X-chromosome of *melanogaster* is short and rod-like, while that of *willistoni* is approximately twice as long and is V-shaped, this relation of the chromosome maps suggests that the *melanogaster* X-chromosome corresponds to one arm of the V-shaped X-chromosome of *willistoni*, with the locus of yellow corresponding in the two cases. This agrees with the suggestion made by Lancefield in the case of *D. obscura* in which the X-chromosomes resemble those of *willistoni*.

8. The comparative lengths of the X-chromosome maps in *melanogaster* and *willistoni* suggests that there is less crossing over in the latter than in the former.

TABLE I

Origin of Mutants

Explanation of "records": W indicates R. C. Lancefield records except numbers 1–100 which indicate D. E. Lancefield; L indicates C. W. Metz; R indicates Ruth Ferry.

Mutant	Symbol	First Found	Record	Parts Affected
1. Stubby........	sy	March, 1920	W 1128	Bristles.
2. Orange........	o	April, 1919	L 37	Eye color.
3. Small-bristle....	sb	July, 1919 July, 1920	L 336 W 1745	Bristles.
4. Bent..........	bn	Nov., 1920	W 1687	Wings.
5. Forked........	f	March, 1919	L 16	Bristles; fertility of females.
6. Forked—2.....	f_2	March, 1920	W 1177	Bristles, hairs; fertility of ♀♀.
7. Tiny..........	t	Jan., 1920	W 856	Bristles.
8. Square.........	sq	Feb., 1920	W 965	Wings; fertility of ♀♀.
9. Reduced.......	re	Oct., 1919	W 288	Bristles; abdomen.
10. Scute..........	sc	May, 1919	L 231	Bristles.
11. Scute—2.......	sc_2	Feb., 1920	W 945	Bristles.
12. Scute—3.......	sc_3	May, 1920	W 1346	Bristles; fertility of ♂♂.
13. Yellow.........	y	Oct., 1921	R 2	Color of body, wings, etc.
14. Peach.........	p	May, 1920	W 1384	Eye color.
15. Beaded........	be	Nov., 1920	W 1964	Wings; viability.
16. Rough.........	r	March, 1919	L 9	Texture of eye.
17. Triple.........	tr	Dec., 1919 May, 1920	W 754 W 1498	Wings.
18. Deformed......	d	Nov., 1919	W 360	Almost every part of body.
19. Serrate........	st	March, 1920	W 1146	Texture and size of eyes.
20. Rimmed.......	ri	May, 1919	W 1	Wings and scutellum; viability.
21. Pale...........	pa	Feb., 1920	W 980	Bristles; viability.
22. Stump.........	s	June, 1919	L 254	Wing vein.
23. Short..........	sh	Feb., 1920	W 1110	Wing veins.
24. Short—2.......	sh_2	May, 1920	W 1440	Wing veins.
25. Short—3.......	sh_3	March, 1920	W 1164	Wing veins.
26. Morula........	m		L 411	Texture of eyes; viability.
27. Nicked........	nk	June, 1919	W 11	Wings.
28. Rosette........	ro	Nov., 1919	L 438	Almost every part of body.

In Tables II–VI parentheses indicate data omitted from the regional summary on account of poor viability of one class or else inability to classify one class. The two columns under the respective headings represent complementary classes, the one to the left that including the normal allelomorph of the gene farthest to the left. *E.g.*, in Table II, experiment 3, under crossovers in region 1 there are 48 normal bristle rough eye flies, and 55 stubby bristle normal eye flies.

The plus sign (+) indicates wild-type or normal.

TABLE II

TWO-POINT CROSSES

Experiment Number	Nature of Cross	Non-crossovers		Crossovers in Region		Total
				1		
3...........	sy r × +	71	73	48	55	247
4...........	o sb × +	1,031	796	34	28	1,886
5...........	o bn × +	285	275	36	25	621
20...........	f × ri	66	70	26	20	182
29...........	sc × ri	304	291	31	29	655
35...........	p r × +	131	81	5	7	224
36...........	p s × +	100	111	20	21	252
38...........	r ri × +	127	73	1	1	202
39...........	r × s	173	170	29	26	398
40...........	s sh$_3$ × +	495	(560)	37	(0)	532
41...........	s × sh	126	(169)	14	(0)	140

TABLE III

THREE-POINT CROSSES

Experiment Number	Nature of Cross	Non-crossovers		Crossovers in Region						Total
				1		2		1, 2		
2..........	sy sb × bn	704	582	28	29	40	38	0	0	1421
6..........	o bn × f$_2$	35	66	6	8	16	8	3	0	142
18..........	f r × re	243	238	40	35	12	25	0	0	593
19..........	f s × sc	48	50	10	9	14	14	1	0	146
23..........	sc ri × r	230	189	20	17	3	3	0	0	462
26..........	sc r s × +	510	460	26	28	55	45	4	2	1130
28..........	sc s × d	258	324	23	25	25	34	1	1	691
32..........	sc ri × m	198	265	42	28	60	26	0	6	625
33..........	sc s sh$_3$ × +	174	(146)	(54)	55	(8)	19	3	(0)	251
34..........	p r × be	(20)	168	3	(0)	(1)	5	0	0	176
37..........	r ri × tr	312	281	2	0	1	5	0	0	601

TABLE IV

FOUR-POINT CROSSES

Experiment Number	Nature of Cross	Non-cross-overs	Crossovers in Region							Total
			1	2	3	1, 2	1, 3	2, 3	1, 2, 3	
1.	sy r × o sb	321 325	9 4	22 12	244 205	0 0	1 1	7 4	0 0	1,156
7.	o re × f s	40 50	15 20	3 13	15 13	1 2	6 5	1 3	0 0	187
9.	o f r × ri	161 150	70 88	58 51	10 2	8 10	2 4	2 1	0 1	618
10.	o r s × t	48 57	30 27	15 23	7 15	5 1	3 3	1 1	2 2	240
12.	o r s × tr	37 56	40 50	0 1	6 7	0 0	8 2	0 0	0 1?	208
13.	o d × r ri	12 19	6 7	0 2	0 2	0 0	0 0	0 0	0 0	48
15.	f re sc$_2$ × r	290 311	54 43	9 4	43 26	0 0	1 0	0 0	0 0	781
21.	re sc$_2$ × be r	(89) 268	1 (0)	4 (0)	(3) 6	0 0	0 0	0 0	0 0	279
22.	sc r s × d	220 160	16 20	8 0	14 13	0 1	1 1	1 0	0 0	455
24.	sc ri × r s	348 306	41 18	6 12	25 17	0 1	3 2	0 0	0 0	779
27.	sc r s × nk	250 306	31 23	42 27	28 10	1 4	3 9	1 19	0 0	754
30.	sc ri × pa m	(38) 108	10 (2)	7 (0)	(6) 7	0 0	0 (1)	0 0	0 0	132
31.	sc ri m × s	149 43	2 15	12 6	12 13	2 2	1 0	0 0	0 0	257

TABLE V

FIVE-POINT CROSSES

Experiment Number	Nature of Cross	Non-cross-overs	Crossovers in Region											Total
			1	2	3	4	1, 2	1, 3	1, 4	2, 3	2, 4	3, 4	1, 3, 4	
8...	o f × sc$_3$ ri s	64 58	27 31	9 9	11 2	6 2	2 2	1 3	3 2	1 0	1 2	1 2	0 0	239
16...	f re × sc r s	167 204	20 18	3 3	8 6	17 28	0 0	0 1	2 1	1 0	1 0	0 0	0 0	480
17...	f re sc$_2$ r × ro	232 222	41 27	1 1	21 14	190 75	0 0	0 0	6 21	0 0	1 0	2 11	1 0	866
25...	sc ri × r s nk	122 140	10 7	2 0	11 0	27 6	0 0	0 2	0 5	0 0	0 3	0 14	0 1	350

TABLE VI

SIX-POINT CROSSES

Experiment Number	Nature of Cross	Non-cross-overs	Crossovers in Region																Total
			1	2	3	4	5	1,2	1,3	1,4	1,5	2,4	2,5	3,4	3,5	4,5	1, 2, 3	1, 2, 5	
11.	o sq r s × sc ri	92 60	41 50	19 4	10 4	2 1	9 9	3 3	2 3	1 2	1 6	0 1	1 1	0 1	2 0	0 0	0 1	0 2	331
14.	f re sc$_2$ r × p s	180 152	16 18	1 1	3 3	11 8	22 18	0 0	0 0	0 1	2 3	0 0	0 0	0 0	0 2	1 0	0 0	0 0	442

TABLE VII

Summary of All Available Data between Consecutive Loci

Region	Cross-over Value	Number of Flies	Region	Cross-over Value	Number of Flies	Region	Cross-over Value	Number of Flies
sy–o[6]	1.3	1,156	t–r[6]	20.8	240	r–d[6]	2.4	503
sy–sb	4.0	1,421	sq–sc[6]	10.6	331	r–ri[6]	2.3	2,742
sy–r	41.7	247	re–sc[6]	0.95	2,848	r–s[6]	11.1	3,444
o–sb[6]	3.5	3,042	re–r	6.2	593	r–ro[6]	35.4	866
o–bn	10.2	763	re–s	23.0	187	tr–ri[6]	1.0	601
o–f[6]	29.0	1,044	sc$_2$–p[6]	1.8	442	tr–s	11.5	208
o–t	30.4	240	sc$_2$–be	1.4	279	d–ri[6]	4.2	48
o–sq	34.7	331	sc–r[6]	7.1	6,388	d–s	7.9	1,146
o–r	44.5	256	sc–d[6]	7.2	691	ri–pa[6]	5.3	132
sb–bn[6]	5.5	1,421	sc–ri	9.9	1,908	ri–s	7.5	1,956
sb–r	40.0	1,156	sc–s	21.9	397	ri–m	14.7	625
bn–f$_2$	19.0	142	p–be[6]	1.7	176	pa–m	5.3	132
f–re[6]	11.2	3,349	p–r	5.0	654	s–sh[6]	7.9	923
f–sc[6]	11.9	385	p–s	16.3	252	s–m[6]	10.1	257
f–r	21.2	618	be–r	2.4	455	s–nk[6]	11.5	1,100
f–ri	25.3	182	r–tr[6]	0.5	809			

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[6] These data were used in the construction of the chromosome "map."